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An insect invasion of Antarctica: the past, present and future distribution of *Eretmoptera murphyi* (Diptera, Chironomidae) on Signy Island

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Abstract. 1. Rising human activity in Antarctica, combined with continued warming of the polar climate, means the risk of non-native terrestrial species colonising and establishing in its biodiversity- and nutrient-poor ecosystems is increasing.

2. Of the five non-native invertebrate species currently in terrestrial Antarctica, the flightless midge *Eretmoptera murphyi* (Schaeffer, The Museum of the Brooklyn Institute of Arts and Sciences 2:90–94, 1914) is perhaps the most persistent insect invader. Accidentally introduced to Signy Island (60°S) in the 1960s from sub-Antarctic South Georgia (54°S), *E. murphyi* has steadily increased its distribution, however, its status has not been reassessed for a decade.

3. Here, we update the distribution of *E. murphyi* on Signy, specifically assessing whether *footpaths* to regularly visited research sites represent dispersal corridors.

4. Our findings show that both the abundance and range of *E. murphyi* have increased significantly since 2009, particularly along paths leading away from the original introduction site, and that the species is now on the cusp of moving into new valley systems.

5. We identify a moderate association with soil/substrate and vegetation types and build Maximum Entropy (MaxEnt) models to predict areas of the island that may be at highest risk of future colonisation.

6. As a detritivore with no competitors or predators, *E. murphyi* may have a major impact. For example, accelerating nutrient cycling which may have wider impacts on all levels of biodiversity.

7. This study highlights the need for an assessment of current biosecurity protocols applied within the Antarctic Treaty system, as well as the need for systematic regular monitoring of introduced and invasive species in Antarctica.

Key words. Biosecurity, distribution modelling, GIS mapping, invasive species, MaxEnt, monitoring.

Introduction

The Antarctic region is the least invaded area in the world, in part thanks to its geographic isolation, harsh climate and limited history of human activity. As a result, few terrestrial species have established naturally in the area south of 60°S latitude since the last glacial maximum (Frenot *et al.*, 2005; Hughes *et al.*,

2015). However, increasing human activity in the region in recent decades – primarily in the forms of tourism and scientific exploration – has diminished the isolation of Antarctica, particularly within the maritime Antarctic, a region encompassing much of the Antarctic Peninsula and the archipelagos of the Scotia Arc. Most recent arrivals of non-indigenous species in the Antarctic region have occurred because of accidental introductions by humans and, as our footprint has increased (Perterra *et al.*, 2016), so records of non-indigenous species becoming established have risen, particularly within the South Shetland Islands and northern Antarctic Peninsula (e.g. Greenslade *et al.*, 2012;

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Volonterio *et al.*, 2013; Hughes *et al.*, 2015; Molina-Montenegro *et al.*, 2012). The few terrestrial introductions that have occurred to date above 60° S latitude have been in, or close to, research stations (i.e. Molina-Montenegro *et al.*, 2010). For example, the introduction of *Lycoriella* sp. (Diptera, Sciaridae), via imported fresh vegetables, to Casey Station on the eastern continental Antarctic (Anon, 2002). Further colonisation of non-indigenous species is likely, given the continuing increase in activity around Antarctica as new research stations are established, and land-based exploration as well as tourism expands. Establishment is then facilitated by predicted changes that an altered and ameliorated climate may bring (Convey, 2011; Chown *et al.*, 2012; McGeoch *et al.*, 2015; Turney *et al.*, 2016). Understanding the biology of established non-indigenous species and monitoring their distributions will be key to understanding how best to control and mitigate this challenge. Only with deeper knowledge of species' physiology, life history, dispersal mechanisms and rate of population expansion, can management and governance processes in the Antarctic be effective in preventing further introductions, as well as minimising the risks of species invasions that have already occurred (Chown *et al.*, 2012; Hughes *et al.*, 2010; Hughes & Pertierra, 2016).

The brachypterous midge *Eretmoptera murphyi* (Chironomidae, Orthocladiinae) (Schaeffer, 1914) is an established non-indigenous species on Signy Island (South Orkney Islands, maritime Antarctic, 60°43'0"S, 45°36'0"W). Native to sub-Antarctic South Georgia, where it is paleoendemic (Allegrucci *et al.*, 2012), *E. murphyi* is thought to have been accidentally introduced to Signy during plant transplant experiments conducted in the 1960s (Burn, 1982; Block *et al.*, 1984). Since its initial discovery on Signy in 1980, it has progressively expanded its range from the original introduction site immediately adjacent to the research station (Burn, 1982; Block *et al.*, 1984; Smith, 1996; Dózsa-Farkas & Convey, 1997; Hughes & Worland, 2010). At some sites, the midge is now found at densities exceeding all other native micro-arthropod fauna combined and, consequently, is influencing litter turnover, with implications for the terrestrial ecosystem and native biodiversity (Hughes *et al.*, 2013). The species is currently considered a *persistent alien* in the absence of direct evidence of impacts on native species, which would lead to it being classified as an *invasive alien* (Frenot *et al.*, 2005).

Eretmoptera murphyi has several physiological traits that have allowed it to succeed in the more extreme maritime Antarctic in comparison to the milder climate of South Georgia. Its larvae have appropriate cold tolerance and can rapidly cold-harden (Block *et al.*, 1984; Everatt *et al.*, 2012; 2015; Worland, 2010), as well as an ability to respire in water and withstand ice entrapment (Everatt *et al.*, 2014). Both eggs and larvae are also desiccation tolerant (Everatt *et al.*, 2014; Bartlett *et al.*, 2018a). The species has a 2-year life cycle and is parthenogenetic – as a result, it does not require synchronous adult emergence and subsequent mating (Bartlett *et al.*, 2018b). This contrasts with its closest relative, the sexually reproducing chironomid and only higher insect endemic to Antarctica, *Belgica antarctica* (Orthocladiinae) (Jacobs, 1900; Sugg *et al.*, 1983). This means that *E. murphyi* can have an extended emergence period across the summer season (Bartlett *et al.*, 2018b), making the most of

environmental windows of suitability, and potentially using this flexibility to increase its distribution range via the more mobile, and more-readily wind dispersed, surface-dwelling adults.

Studies of the distribution and abundance of *E. murphyi* on Signy have only recently begun in earnest, with the benchmark survey of Hughes and Worland (2010), which took place in 2007–2009, c. 40 years after the suspected introduction, and 25 years following its initial discovery (Burn, 1982). Hughes and Worland (2010) provided the first comprehensive assessment of the spread of *E. murphyi* around its original introduction site and found densities as high as 150 000 larvae m⁻² (Lm⁻²), with evidence of the midge being more prevalent along paths leading away from this area. These data suggested that although flightless, adults may be capable of dispersal to some extent. However, it is the mechanical process of human footfall and disturbance of larvae in the soil that could be a key factor facilitating its spread – as has also been noted for non-indigenous plant species in Antarctica (Molina-Montenegro *et al.*, 2012). While Hughes and Worland (2010) did not identify the limit of the species' distribution, their study confirmed that *E. murphyi* had spread to cover an area of at least 35 000 m², doubling the previous estimate made in 1995 (Dózsa-Farkas & Convey, 1997). The survey noted a highly patchy distribution pattern, with *E. murphyi* typically associated with dead organic matter, rather than live moss or inorganic substrates such as gravel and rock. This is consistent with *E. murphyi* being a detritivore (Cranston 1985; Hughes *et al.*, 2013). However, as yet, no robust assessment has been made of the availability and extent of suitable habitats for *E. murphyi* around the island, or how species abundance changes across different substrate types, i.e. evidence of substrate preference.

Species distributions and relationships with associated habitats have typically been analysed using correlative models that use linear and/or logistical regressions to establish the main drivers of species abundance (Wiens *et al.*, 2009; Porfirio *et al.*, 2014). Developments of open source software, using geographical information, now allow ecologists to use known species presence (and absence) data in combination with environmental niche predictors to more accurately model likely changes in distribution (Rushton *et al.*, 2004; Raghavan *et al.*, 2016). Such models can aid understanding of species responses to climate change (e.g. Wang *et al.*, 2018), help assess extinction rates (e.g. Thomas *et al.*, 2004), identify habitat loss scenarios (e.g. Angelieri *et al.*, 2016), and prioritise biological conservation efforts (Pyke *et al.*, 2005). They can also be used to forecast suitable areas for the spread of an invasive species (West *et al.*, 2016; Pertierra *et al.*, 2016) through estimations of *probability of presence* given a series of biotic and/or abiotic variables such as terrain, habitat classification, temperature or dispersal vectors.

Antarctica is a globally important reservoir of unique ecology and biodiversity, and Signy Island provides the best example of terrestrial biodiversity in the region. As a non-native detritivore in such high abundance, *E. murphyi* may alter the Signy Island ecosystem, and areas beyond if given the opportunity to disperse. Few studies to date have examined Antarctic invertebrate invasions in depth, with no regular monitoring of long-term abundance

and distribution changes of those species that have colonised. In this study, we map the current distribution of *E. murphyi* across Signy Island and evaluate the role of footpaths as dispersal corridors. We establish its association with preferred environments through physical study of its habitat and, using Maximum Entropy (MaxEnt) species distribution modelling, highlight areas at risk of further colonisation across Signy Island.

Materials and methods

Signy Island is located in the South Orkney Islands archipelago in the maritime Antarctic, ($60^{\circ}43'S$, $45^{\circ}36'W$; Figs. 1 and 2). The island is 6×5 km in size, with a maximum elevation of 288 m across a small mountain range that holds its large ice cap. Signy experiences slightly positive temperatures for most of the austral summer (December to March) with monthly averages of $+1$ to $3^{\circ}C$. During winter, the island is surrounded by sea ice extending from the Antarctic continent and temperatures remain far below freezing, with a winter average of $-10^{\circ}C$. Rising temperatures throughout the Antarctic Scotia Arc region mean that the island is de-glaciating and consequently much ice-free land is experiencing primary succession.

Extent of *E. murphyi* distribution

Distribution surveys were primarily conducted along frequently used paths radiating from the British Antarctic Survey (BAS) research station on Signy. In total, 14 *stop-sites* were sampled along the *High-tide* (HT) and *Stonechute* (SC) paths (Fig. 2), with soil cores taken at 1 m and 5 m distances perpendicular to the path, every $20 \text{ m} \pm 2 \text{ m}$ (measured using a tape reel). Where the path broadened away from the sea, samples were taken on either side of it at both 1 m and 5 m, respectively. Otherwise, all samples were taken to the inland side of the path, with the final *stop site* at the summit of the SC. Fourteen *stop sites* were also sampled along the *Backslope* (BS) path (Figs. 1 and 2), following the same procedure, and sampling on both sides of the path, with the final *stop site* at the summit plateau between Factory and Observation Bluffs. *Whole island* survey routes targeted potential habitat of *E. murphyi* (moss patches or banks) at $c. 50 \text{ m}$ intervals (closer if habitat irregular), taking cores from each site (Fig. 2). These routes followed the frequently used paths from the top of the SC to the huts on the Goulay Peninsula (GP trail) where regular penguin colony monitoring has been conducted for over 30 years (14 sites sampled) and from the top of the SC to the cemetery flats (CF) crossing, which is the main access route to freshwater lakes and other parts of the north and west of the island (7 sites

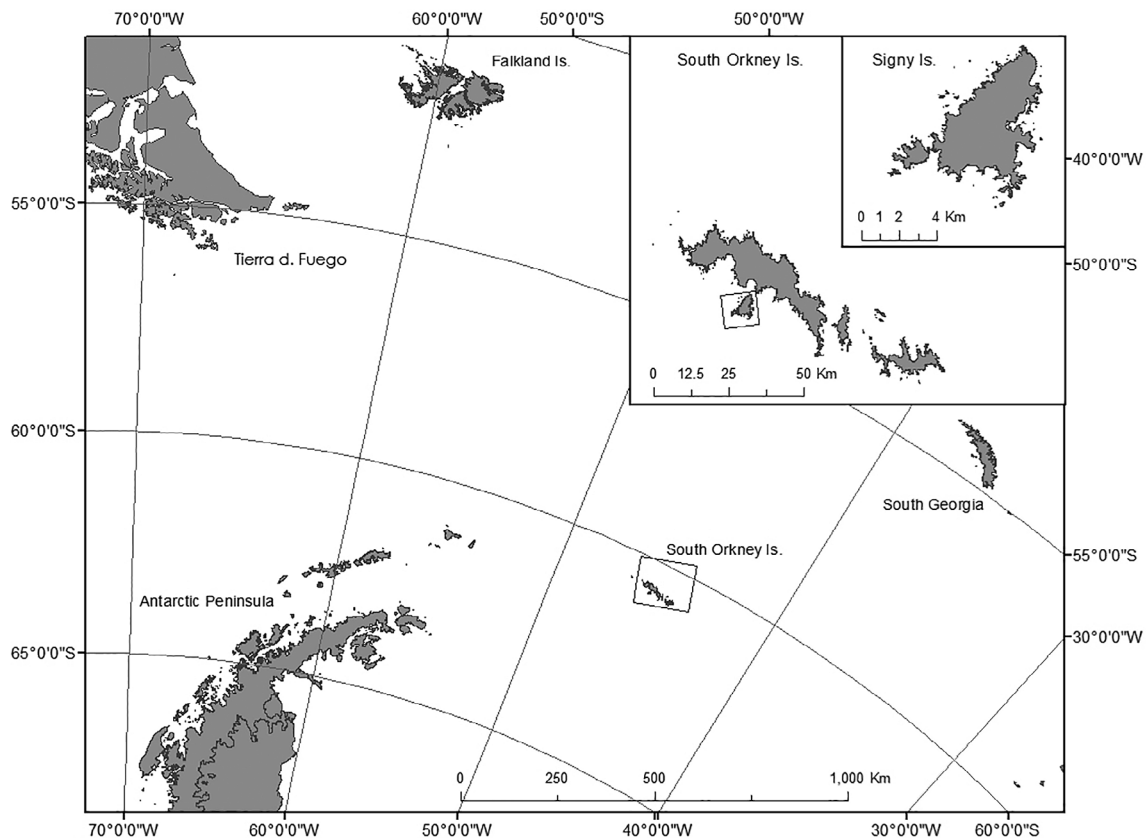


Fig. 1. The location of Signy Island, in the South Orkney Islands archipelago off the north-east tip of the Antarctic Peninsula. $60^{\circ}43'0"S$, $45^{\circ}36'0"W$. Created using ArcMap[®] 10.4.1 software by Esri.

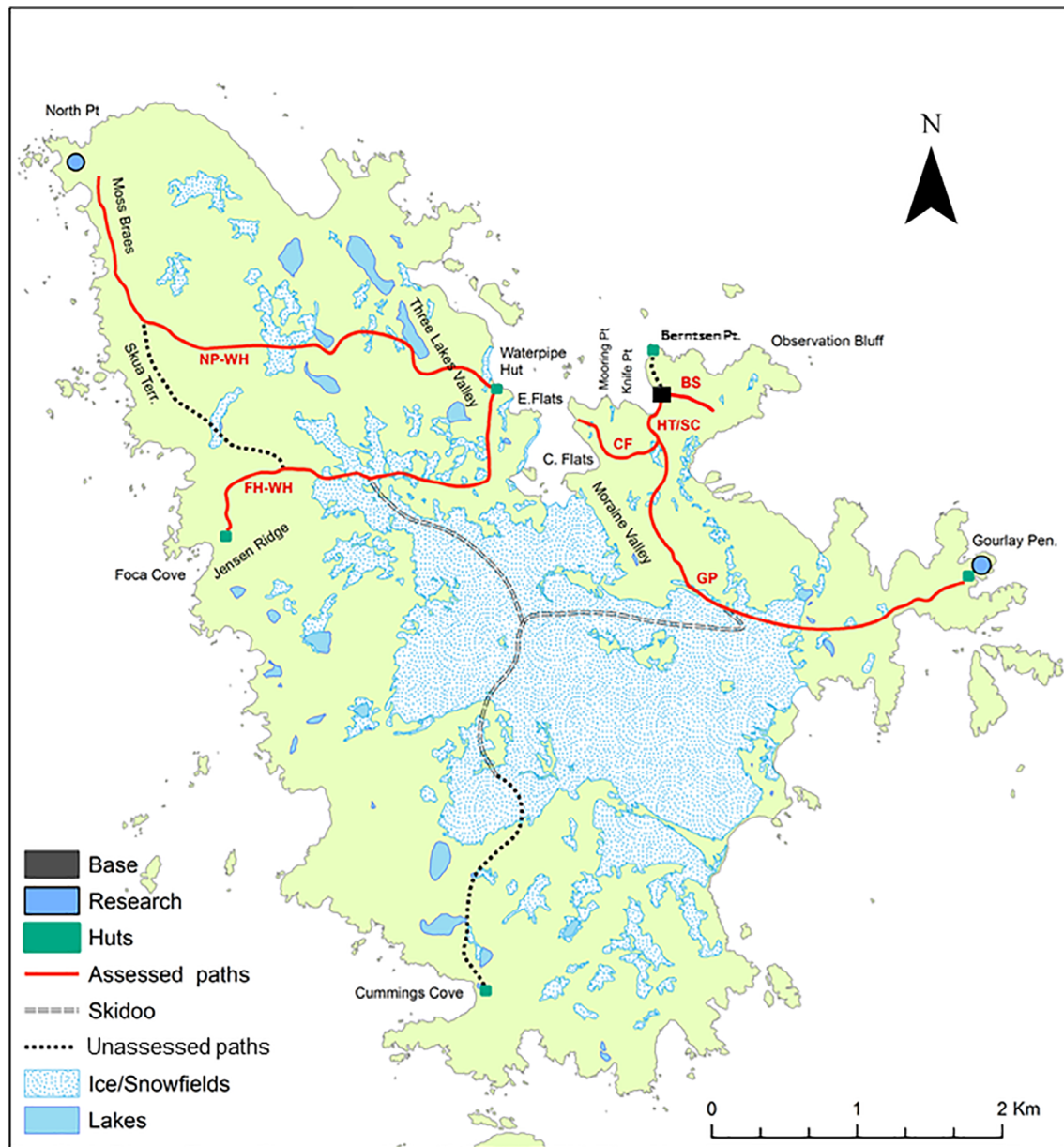


Fig. 2. Map of survey routes across Signy Island, shown with regular research sites, shelter huts and the research station. Discussed locations annotated in black, whilst abbreviations for survey routes shown in red (see main text for full names). [Color figure can be viewed at wileyonlinelibrary.com]

sampled). Further routes were surveyed from Waterpipe Hut (WH) over Jane Col to Foca Hut (FH) on the west coast of the island (16 sites sampled), and from North Point (NP), where penguin and bird survey work is currently conducted several times a season, over Spindrift Col and down to WH (Fig. 2, 10 sites sampled). These latter routes reflect historically well-used paths around the island. Focus was given to sampling close to the field huts established on the island.

In addition to the survey routes, a grid of points 100 m apart was plotted over the entire area adjacent to the research station, covering an area of 490 000 m², in order to establish the extent of *E. murphyi*'s distribution (Fig. 4). This *edge of extent* grid

incorporated Berntsen Point at its northern-most point, extended several meters beyond the summit of the SC path at its southern-most point, Observation Bluff and Gash Cove to the east, and as far as the gully between Mooring and Knife Points to the west. As previously, soil cores were sampled at each grid point and analysed for presence of *E. murphyi*.

Sample collection and processing

Soil cores ($n = 3$) were taken from each designated sample point, using a steel 2.5 cm ϕ , 10 -cm long soil corer, with all cores

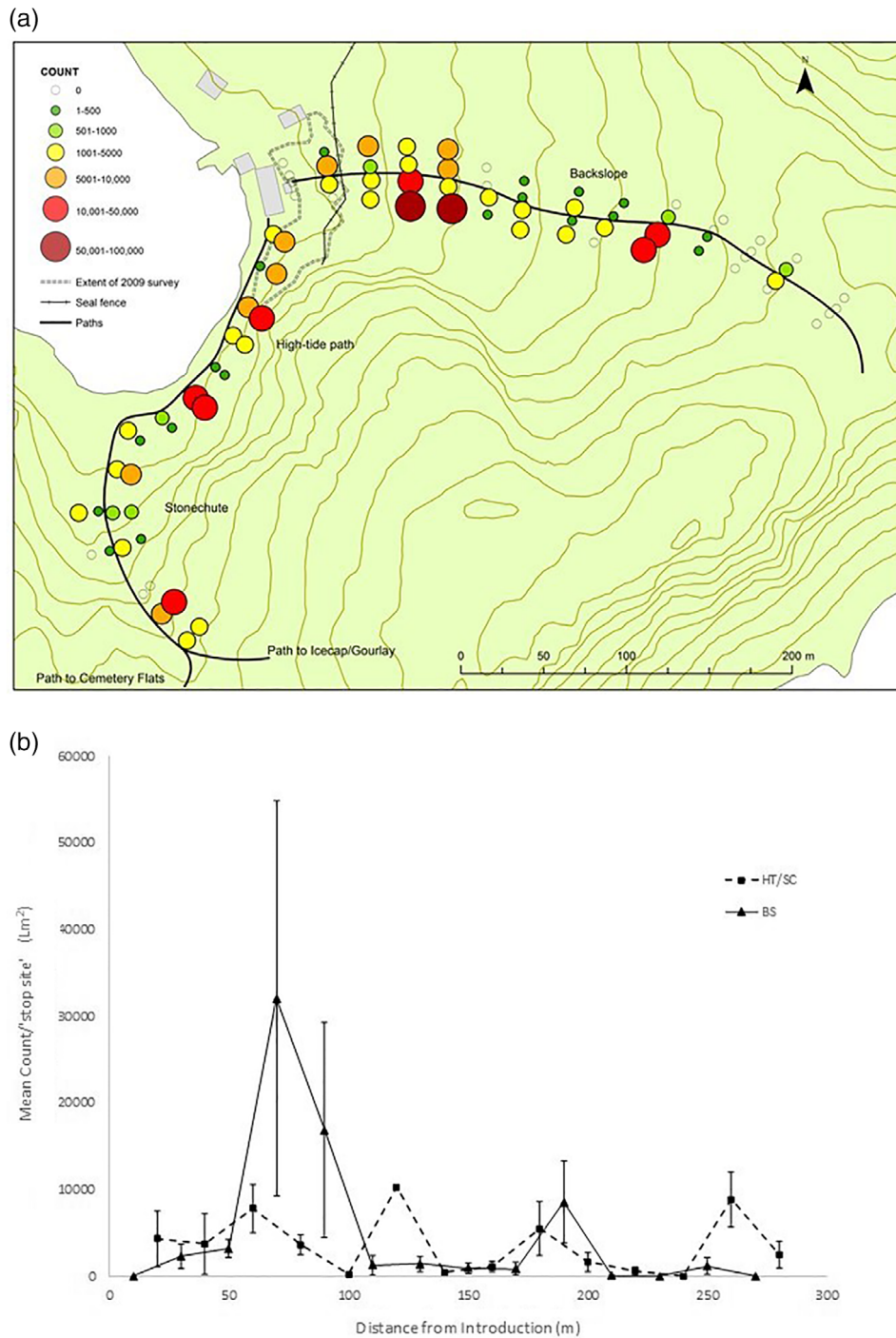


Fig. 3. (a) Abundance and distribution of *E. murphyi* in the 2016/17 season along and adjacent to the Backslope (BS) path and the High-tide (HT)/Stonechute (SC) paths. Shown with the outline of 2009 survey (Hughes & Worland, 2010). Circles represent the mean number of larvae per m². (b) Mean abundance (\pm SEM) per 'stop site' along each of the two routes (BS and HT/SC), and their approximate distance from the original introduction site (adjacent to the research station). [Color figure can be viewed at wileyonlinelibrary.com]

returned to the Signy laboratory in individual sterile sealed bags. Samples were collected during the 2016/17 austral summer and returned to the United Kingdom by ship in +4 °C cold storage (10 weeks) and then maintained at +4 °C at the University of

Birmingham until analysis. All samples from areas of known/likely distribution (HT, SC, BS and Edge of Extent Grid) were analysed within 6 months of initial collection. Further *Whole Island* routes were analysed within 1 year of collection. Individual

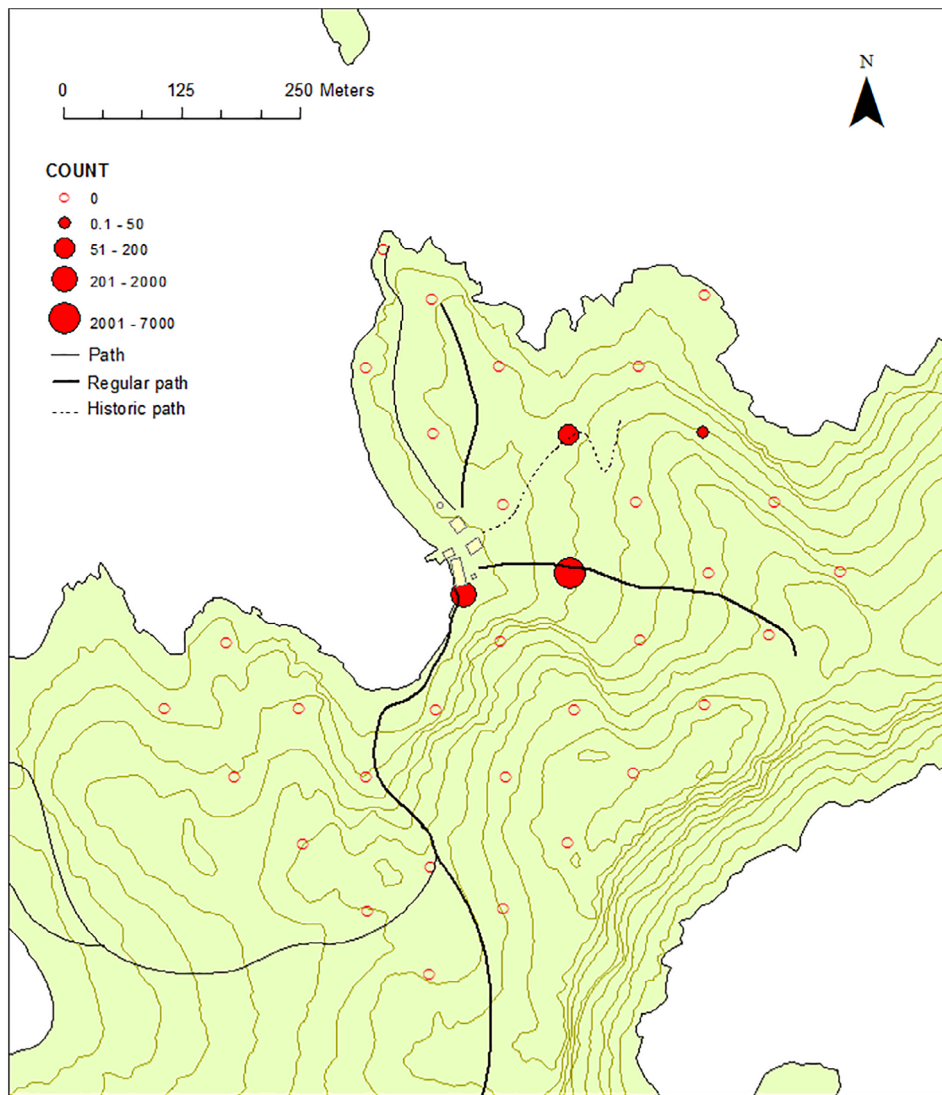


Fig. 4. Map showing the *edge of extent* grid and associated abundance. Circles represent the mean number of larvae per m^2 . [Color figure can be viewed at wileyonlinelibrary.com]

larvae that were visible by eye (instars 2–4, L2–L4) and egg sacs were extracted from the substrate by washing through stacked sieves (2, 0.5, 0.25 mm mesh sizes) and hand-picked from the remaining soil on the 0.25 mm sieve, with the 0.5 mm sieve checked for any further individuals. L1 larvae could not be included in this survey due to their very small size. Prior to washing, any clumps of moss or peat substrates were teased apart with tweezers, freeing any individuals that may have been amongst the fibres.

The constituent parts of each core's upper and lower dominant substrate components were noted for subsequent correlation analysis with *E. murphyi* abundance. Substrates were divided into 10 sub-types, six for the upper substrates and four for the lower (Table 1). Larval densities were expressed as the mean for each set of three cores. Egg sacs were also included, with

their larval potential calculated using known egg hatching success rates (cf. Bartlett *et al.*, 2018a) (Eqn. 1). Densities per metre square were estimated by calculating the surface area of the corer and scaling up (cf. Hughes & Worland, 2010). This gives a multiplier of 1949 to apply to the combined counts of larvae (L) and larvae from egg sacs (E_L) to obtain a count of larvae per m^2 (Lm^{-2}).

$$E_L = (E_g \times E_s) \times E_h \quad (1)$$

where E_L is the calculation of larvae produced from egg sacs, E_g is the mean egg sac count for three cores, E_s is the mean eggs per egg sac (48*), and E_h is the % eggs that hatch (based on 35% successful hatch rate*) *after Bartlett *et al.* (2018a).

Table 1. Substrate type for upper (Ux) and lower (Lx) core constituents.

	Soil	Peat	Moss	Vascular	Algae	Inorganic
Lower	Ls	Lp	Lm	<i>n/a</i>	<i>n/a</i>	Li
Upper	Us	Up	Um	Uv	Ua	Ui

Statistical Analysis and Data Visualisation

In order to determine any correlation between substrate type (see Table 1) and the abundance of *E. murphyi*, two regression methods were employed. Firstly, mean abundance per m² (for BS and HT/SC paths) were Log₁₀ transformed and plotted against the binary presence/absence data for each substrate type and then investigated for significant substrate types associated with *E. murphyi* abundance using an ordinal logit regression (OLR) (XLStat, verified with SPSS) by categorising the population abundance per m² into the following categories: zero, low (1–1000), medium (1001–10 000), and high (10 001–100 000). Whilst this provided a good model on what were the significant relationships, further detail was required, so a general linear model (GLM) was run on the Log₁₀ transformed data (XLStat) to obtain a true *R*² value for substrate type – abundance relationships. Upper inorganic (Ui) substrate had zero observations, whilst upper vascular (Uv) and upper algae (Ua) had just one each, so were removed from the subsequent analyses. Both methods produced the same significant substrate type abundance relationship, validating one another and the decision to take the significant substrates forward into the maximum entropy model.

MaxEnt Modelling for Whole Island Colonisation Risk

Maximum entropy species distribution modelling (MaxEnt) (Phillips *et al.*, 2006) is a common technique used to model a species' potential distribution based on the known geographic distribution and associated environmental background information. Its application here allows identification of similar areas to those already occupied by *E. murphyi*, indicating the relative potential for establishment. MaxEnt v3.4.1 (http://biodiversityinformatics.amnh.org/open_source/maxent/) was used to model colonisation risk for areas of the island with input layers created as follows: using a digital elevation model (DEM) of Signy Island, GIS raster layers with a cell size of 5 m² were generated for aspect, slope and altitude. Using this topographical information, the programme output identified preferential habitats for *E. murphyi* presence across the island, based on the locations of its current distribution. This layer of topographical preference for *E. murphyi* occurrence was then combined with other raster layers to account for human activity around the island; preferred substrate type (i.e. findings from abundance-substrate-type correlations set out above) and distance from the current distribution of *E. murphyi*. All raster layers were created in either ArcMap 10.4.1 or QGIS v2.18 *Las Palmas* (QGIS Development Team 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>). Human footprint was classified into nine categories

from very high to infrequent/nil (Supporting Information Online Resource 1), based on a subjective assessment of the level of activity in an area in any one season on the island, derived from discussions with, and observations of Signy Island research personnel during the 2016/2017 season. The distance layer was created using Euclidean distance interpolation, radiating from the area of current *E. murphyi* presence as defined in this study. The substrate type layer was constructed based on the results of the OLR/GLM modelling and presence/absence of the substrates preferred by *E. murphyi*. Terrain models selected environments of similar aspect, slope and altitude to those where *E. murphyi* is verified to be present in order to predict further at risk areas. As true absences were also recorded during the whole island and edge of extent surveys, it was not necessary to generate pseudo-absences for the model. The final distribution map was then created in ArcMap 10.4.1, with added landscape features and sites of significance. Areas of the island currently covered with ice or permanent water bodies were discounted as areas at risk and masked out accordingly.

Results

Local distribution and abundance of *E. murphyi*

Figure 3a shows that the distribution of *E. murphyi* now extends well beyond the immediate area of the research station (RS), and it can be found in densities of up to 12 000 Lm⁻² close to the summit of the SC path, 240 m beyond the RS. Abundance lower down the path is equally high, with several points exceeding 10 000 Lm⁻². The highest densities were found on the BS path, reaching 98 241 Lm⁻² at 40 m and exceeding 50 000 Lm⁻² at 60 m.

Densities reduced further up the path, although still sporadically with densities >10 000 Lm⁻² after ~100 m. The mean densities along the HT/SC and BS paths were not significantly different (HT/SC mean 3317 Lm⁻² ± 671 SEM, *n* = 32; BS mean 4904 Lm⁻² ± 2031 SEM, *n* = 56; *p* = 0.56, unpaired *t*-test). Combining the data across both paths, 28% of sample points gave zero counts, 27% low counts (1–1000), 35% medium counts (10 001–50 000) and 10% high counts (50 001–100 000).

Eretmoptera murphyi population density did not differ significantly with increasing distance from the path (*p* = 0.31, Mann–Whitney). However, there was a small (but non-significant) decline in density further from the introduction site (BS – *R*² = 0.09, *p* = 0.2; HT/SC – *R*² = 0.03, *p* = 0.5) (Fig. 3b).

Edge of distribution and whole island survey

The 100 × 100 m edge of extent grid (Fig. 4) found evidence of *E. murphyi* along both currently used and historic paths, with a small number of larvae found on a ridge south-east of the old study site path, over 300 m from the original introduction site. Surveys of other paths around the island found no evidence of *E. murphyi* presence (see Supporting Information Online Resource 2).

Substrate type distribution and E. murphyi substrate preference

Different substrate types (table 1) differed significantly in frequency across collection sites ($p < 0.001$, Kruskal–Wallis). This was largely driven by the dominance of moss in the upper part of substrate cores (Um = 43%) and soil in the lower core (Ls = 30%). The most common habitats were those of moss banks: Um/Ls (55%) and Um/Lp (14%), whilst the least observed combinations (excluding Us/Lm and Up/Lm which were totally absent) were those of bare ground/peat (Table 2). Results for the OLR found that only soil and peat in the lower core (Ls and Lp, respectively) had a significant positive association with *E. murphyi* density (Ls, $p = 0.032$; Lp, $p = 0.024$) (Fig. 5). These two substrates explain 10% of density variability through a GLM ($R^2 = 0.10$, $p = 0.011$). Additional results from the GLM and associated correlation matrix indicated that Ls was the most significant of the two substrate types ($p = 0.003$). Further analysis of substrates along footpaths around the island, found suitable habitats (moss banks with soils and peat in the lower core: Um/Ls or Um/Lp,) for *E. murphyi* colonisation around Cemetery Flats, the Gourlay Peninsula and Three Lakes Valley in particular.

MaxEnt Modelling for Whole Island Colonisation Risk

Results from the MaxEnt model (Fig. 6; Supporting Information Online Resource 3) indicate that, beyond the area of known distribution, the areas of highest overall risk are Berntsen Point, Observation Bluff, Cemetery Flats and the areas of Mooring and Knife Points, and the trail through Moraine Valley. Medium – high-risk areas include parts of the Gourlay Peninsula, Elephant Flats, Waterpipe Hut and Three Lakes Valley. Areas at a medium risk of establishment are largely found in patches around Moss Braes near North Point, parts of Skua Terrace, Jensen Ridge and Foca Cove, and areas close to Cummings Hut. Of the environmental variables taken from the DEM, aspect explained 65% of the known distribution envelope of *E. murphyi*, with slope 25% and altitude 10%.

Discussion

With the increasing risk of non-native species colonising Antarctic terrestrial habitats, there is an urgent need to regularly assess the rate at which successful invaders can extend their distribution, whilst also assessing their preference for available habitats in order to best forecast other areas that may be at risk. This study represents the most comprehensive survey of the flightless midge *E. murphyi* on Signy Island to date. This species has extended 85 000 m² beyond its presumed introduction site in the 1960s, and we report distributions totalling 50 000 m² beyond the limit of the last survey in 2009 (Hughes & Worland, 2010) (Fig. 7). Thus, while its spread began slowly, it has clearly accelerated in recent years. The importance of human footfall along routes to regularly visited research sites is further supported as a likely means of dispersal.

Table 2. Combination of occurrences for each substrate type (see Table 1) in the upper and lower core, with the most positive (in bold) or most negative (italics) associations with *E. murphyi* abundance (R^2) shown along with related significance ($*p < 0.01$). See Table 1 for definition of acronyms.

Substrate combination	Habitat description	% Occurrence (BS and HT/SC combined)
Us/Lm	-	0
Up/Lm	-	0
Us/Lp	Soil on peat – bare ground/peat	1.15
Up/Ls	Peat on soil – bare ground/peat	1.15
Up/Lp	Peat core – bare peat	2.3
Up/Li	Peat on stone – bare peat	2.3
Us/Ls	Soil core – bare ground	3.45
Us/Li	Soil on stone – bare ground/fellfield	3.45
Um/Li	Live moss on stone – recent succession	6.9
Um/Lm	Live moss bank core – established moss peat bank	9.2
Um/Lp	Live moss on peat – moss peat bank	15
Um/Ls*	Live moss on soil – recent succession/ organic breakdown	55.1

This survey doubles the known range of *E. murphyi* since the previous survey conducted a decade ago. The highest population densities were found on the Backslope (BS) path immediately behind the Research Station (RS) (Fig. 3b), with a steady but small decline after this point with distance up the path. Densities along the high-tide (HT)/Stonechute (SC) path were patchier, but densities of $>1000 \text{ Lm}^{-2}$ persisted along this route. There was no discernible difference in the substrate types between the two paths, but the HT/SC path is used by personnel on a more frequent basis than the BS, which may account for the higher abundance further along this path.

The combination of methods used here, targeted surveying (path transects) and systematic surveying (extent grid), illustrates the value of both techniques, with the targeted survey highlighting details of density patterns, and the systematic grid locating outlying populations, as well as habitats where the species currently remains absent. We recommend that both methods are used in future monitoring of *E. murphyi* on Signy as a minimum requirement in assessing changes in abundance and distribution over the largest area possible. Such combined approaches to non-indigenous species monitoring are also recommended as best practice by Rew *et al.* (2006) in their comprehensive analysis of survey methods used for the monitoring of invasive plant species in the United States. Furthermore, they recommend that all monitoring of species distribution and abundance coincides with the collection of habitat data, such as we have demonstrated here in characterising substrate type and topography, to ‘improve our understanding of factors affecting NIS (*sic*, non-indigenous species) occurrence, and to produce probability occurrence maps of target species’.

Regression analyses identified that, whilst live moss in the upper part of the sampled cores (Um) and soil in the lower part (Ls) were the most abundant substrates, it was the presence of

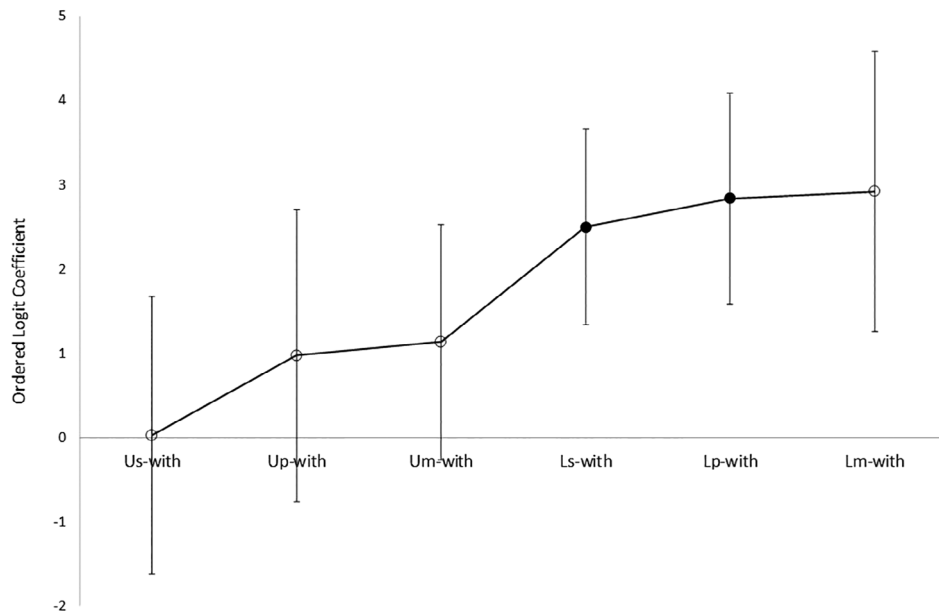


Fig. 5. Results of ordinal logit regression (OLR) – key substrate types (Table 1) as values of ordered logit coefficient, plotted in order of least to largest influence on *E. murphyi* abundance (\pm SEM). Substrate types testing significant through the OLR ($p < 0.01$) shown as solid fill circles. All variables >0 plotted.

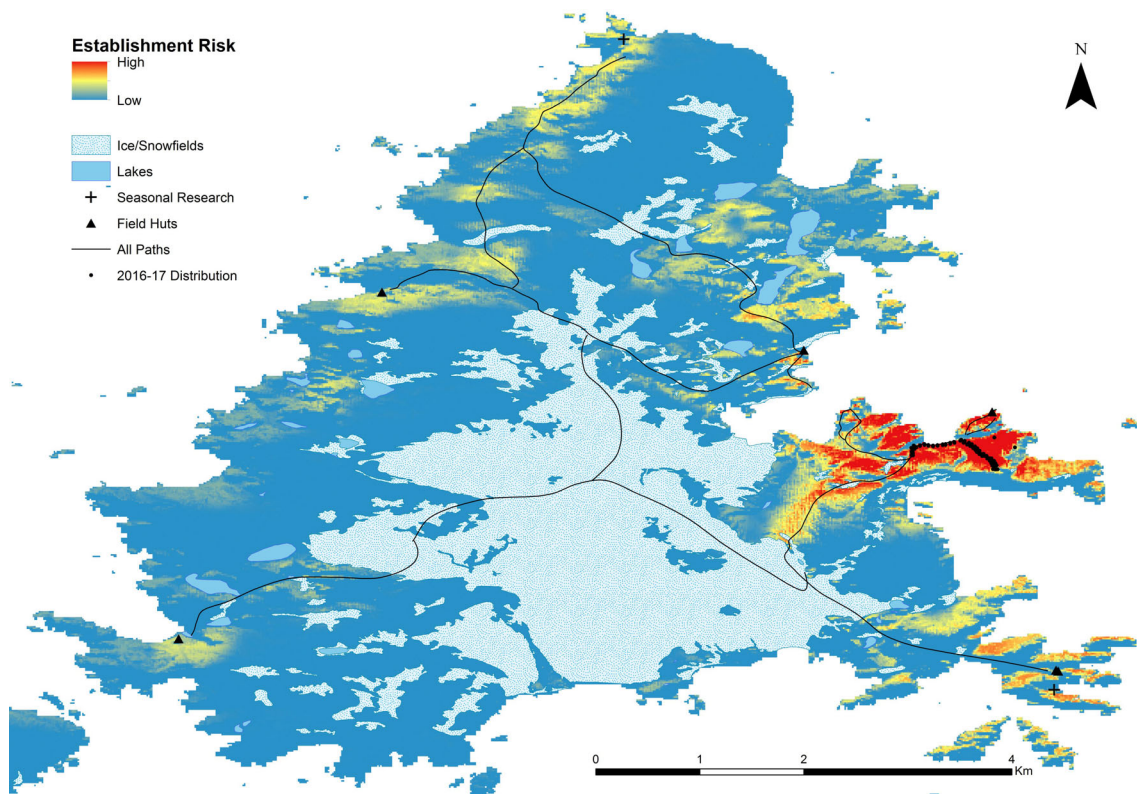


Fig. 6. Results of MaxEnt model showing the establishment risk of *E. murphyi* around Signy, based on its 2016/17 distribution, available habitat and human footfall around the island. Also shown are all paths (including skidoo routes across the ice cap), field huts and seasonal research sites. Model visualised using ArcMap 10.4.1 with raster symbology using $n = 6$ SD and Gamma stretch = 1.5. [Color figure can be viewed at wileyonlinelibrary.com]

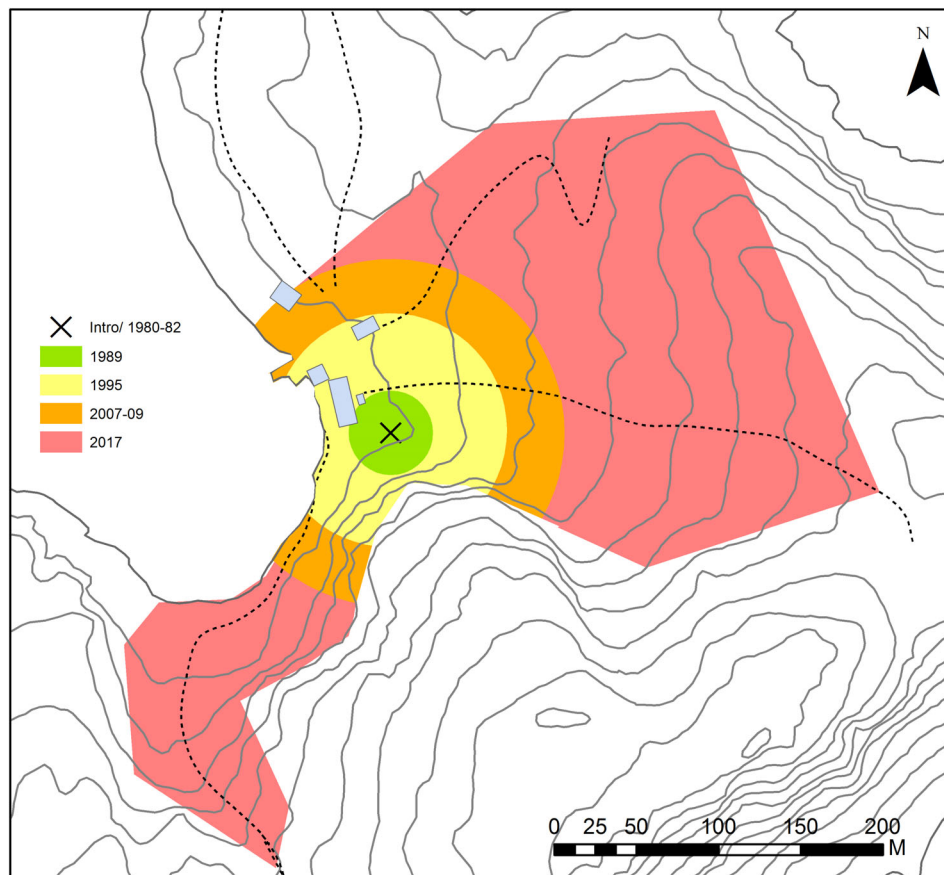


Fig. 7. Spread of *E. murphyi* over time: Introduction site and initial recordings of presence (Burns, 1982; Block *et al.*, 1984); 1989 distribution $\sim 200 \text{ m}^2$ (Smith, 1996); 1995 distribution $\sim 16\,000 \text{ m}^2$ (Dozsa-Farkas & Convey, 1997 – calculated as radius); 2007–2009 distribution $\sim 35\,000 \text{ m}^2$ (Hughes & Worland, 2010 – calculated as radius); 2017 distribution, this study $\sim 85\,000 \text{ m}^2$ calculated as exact polygon from areas of known presence. [Color figure can be viewed at wileyonlinelibrary.com]

soil and peat in the lower part of the cores that had the strongest correlation to *E. murphyi* population density. This is consistent with *E. murphyi* being a detritivore. Hughes and Worland's (2010) data also support the negative association of *E. murphyi* with both live moss and inorganic substances such as stones and gravel in the lower core identified in this study. However, substrate type explained only 10% of variation in density, making it likely that other factors are primary drivers of population density and distribution. It also remains unclear if the association of *E. murphyi* with soil and peat is because of preference for this habitat, or because the midge is generating the soil substrate type and aiding decomposition of the existing moss and vegetation.

Population densities over $12\,000 \text{ Lm}^{-2}$ close to the summit of the SC path, and of 1000 Lm^{-2} 1 m from the path at the summit (Fig. 3b), suggest that this species could be on the verge of entering into new valley systems. This is of concern given the availability of prime habitat leading down to cemetery flats (CF). If able to establish in the CF area, the risk of wider spread will be increased by the seal populations there. Fur seals in particular are very mobile, disrupting the moss bank surface as they move (Favero-Longo *et al.*, 2011), and there is the potential that larvae

and eggs may be carried in their fur, particularly the egg sacs that have a sticky gelatinous outer membrane (Bartlett *et al.*, 2018a). Results from the MaxEnt model suggest that combinations of suitable habitat and human footfall are frequent through the ice-free areas of the island, but that primarily the areas of CF and the Gourlay Peninsula (GP) are most at risk of further colonisation, largely because of their proximity to the existing distribution of *E. murphyi*.

Older and less used paths have no trace of *E. murphyi* on them at present (Supporting Information Online Resource 2) yet do have suitable habitats as identified by both MaxEnt and along-route sampling. The large moss and peat banks of Skua Terrace and Moss Braes in particular (Fig. 2) present a large area of potential habitat (Cannone *et al.*, 2017), especially where live moss does not extend too deeply. In addition, if larvae or eggs could survive a short low-tide crossing from CF – where researchers (and seals) quickly move through shallow sea water and pools to access the northern part of the island – then much of the area around Waterpipe Hut (WH) and Three Lakes Valley would also become accessible for colonisation, with Elephant Flats and soils directly surrounding WH at particular risk.

Within the wider region of the maritime Antarctic, favourable climate and habitats for *E. murphyi* have been identified in the South Shetland Islands and along the western coast of the Antarctic Peninsula, with islands in Marguerite Bay close to Rothera Research Station at particular risk (Hughes *et al.*, 2013). The indigenous and endemic chironomid *B. antarctica*, which already occurs across this region, favours similar habitats to *E. murphyi* and has generally similar physiological capabilities (Edwards & Baust, 1981; Sugg *et al.*, 1983; Convey & Block, 1996; Lee *et al.*, 2006; Benoit *et al.*, 2007; Everatt *et al.*, 2012, 2015). Therefore, any expansion of *E. murphyi* into this region could result in impacts on, or even displacement of, *B. antarctica*, particularly given the possible advantage gained from *E. murphyi*'s more flexible parthenogenetic life history strategy (Bartlett *et al.*, 2018b).

Hughes *et al.* (2013) concluded that *E. murphyi* was significantly affecting litter turnover on Signy Island. With a biomass at some sites of two to five times that of the estimated indigenous micro-arthropod and micro-invertebrate community (mites, springtails, tardigrades, nematodes and rotifers), a mean *E. murphyi* population of $21\,000\text{ Lm}^{-2}$ could increase litter turnover by as much as $66.51\text{ g dry mass m}^{-2}$ per annum. This is almost a full order of magnitude (9.3 times) the consumption rate of the native Signy community (*cf.* Davis, 1981). In an analogous study, Hänel and Chown (1998) found that another invasive chironomid, *Limnophyes minimus*, on sub-Antarctic Marion Island, was also increasing litter turnover by 6–10 times the rate of the larvae of the native moth *Pringleophaga marioni*, superseding it as a major contributor to the island's nutrient cycling. As *E. murphyi* is the only macro-invertebrate on Signy Island and has no predators or competitors, its impact on the terrestrial ecosystem is likely to be unimpeded. Furthermore, as *E. murphyi* develops greater population densities (Hänel & Chown, 1998; Hughes & Worland, 2010; this study) and is physically larger than *L. minimus* (*cf.* Mercer *et al.*, 2001), it is likely to be one of the most significant introductions to a sub-or maritime Antarctic terrestrial ecosystem yet recorded.

The accidental introduction of *E. murphyi* to Signy Island is not a unique case for Antarctica but does represent perhaps the most successful and best studied invertebrate introduction outside of the sub-Antarctic region to date. Introduced to Signy with *E. murphyi* was the enchytraeid worm, *Christensenidrilus blocki* (Block *et al.*, 1984), which remains persistent but far less abundant or widely distributed (Hughes & Worland, 2010). In neither instance was eradication attempted, with initial studies instead focusing on the physiology of *E. murphyi* (e.g. Block *et al.*, 1984), rather than the risks it might pose as an invasive species. Now the distribution of *E. murphyi* is so extensive that eradication is not feasible without considerable and unacceptable damage to the larger ecosystem. Within the maritime Antarctic, another dipteran species, *T. maculipennis*, was also recently accidentally introduced to King George Island in the South Shetland Islands – this species was first discovered around the Uruguayan Artigas Base in 2006 and previously had only been recorded in the Northern Hemisphere (Volonterio *et al.*, 2013). Eradication of this species from the affected sewage system has been attempted on more than one occasion but has not been successful (Uruguayan Antarctic Institute, 2008; Volonterio *et al.*,

2013); meanwhile, further stations have been affected on the island (Potocka & Krzemińska, 2018). Whilst invertebrate introductions are increasingly frequent in the Antarctic and sub-Antarctic areas (Chown *et al.*, 2012, b), it remains the case that, to date, only *E. murphyi*, *C. blocki* and *T. maculipennis* have successfully established within the maritime Antarctic region for any duration.

The in-depth monitoring of *E. murphyi*'s spread within the current study has identified a potentially imminent risk to other valley systems on Signy Island. However, such monitoring of non-native invertebrate species is not currently required either as an advisory or a mandated requirement within either the Antarctic Treaty area or the various sub-Antarctic islands. Transfer in soil and associated vegetation is a known means of anthropogenic transfer of *E. murphyi*, with such an event already having taken place from the species' native South Georgia to Rothera Research Station at 68°S on the Antarctic Peninsula, via the treads of industrial plant equipment (Hughes *et al.*, 2010). Current measures used to prevent the transfer of biological material into the Antarctic region and between different Antarctic locations, primarily rely on manual scrubbing of boots and equipment, and a boot wash containing the antimicrobial/viral disinfectant Virkon-S (SCAR 2009; IAATO Guidelines, 2018; BAS Biosecurity Regulations 2018). The efficacy of these measures in preventing invertebrate transfer, however, is unknown, and Virkon-S has never been formally tested as an insecticide. We suggest that it would be prudent to re-evaluate existing biosecurity procedures, such as recommended by Hughes and Pertierra (2016) and subsequent ATCM proposal (ATCMXLI-IP31 United Kingdom and Spain, 2018). A further species that would benefit from such regular monitoring would be the invasive predatory beetle *Trechisibus antarcticus* on South Georgia which, ironically, may have drastically reduced *E. murphyi* populations in its native range, along with other endemic invertebrate species (Ernsting, 1995; Convey *et al.*, 2011). Its current distribution, and thus the magnitude of its impact on South Georgia's terrestrial invertebrate communities, remains unknown and unchallenged.

Conclusions

Eretmoptera murphyi has significantly expanded its range on Signy Island over the last decade, and this appears to be in direct association with routes of human movement across the island. The species' preferred habitat is moss bank with soil and peat substratum layers, largely on a northerly aspect, although this preference only explains a small proportion of variation in its population density. It is also unclear whether *E. murphyi* is selecting existing peat substrates or actively driving the production of peaty soils. A pre-adapted physiology to survive maritime Antarctic conditions and life history features that permit a flexible and opportunistic phenology, combined with anthropogenic intervention, has enabled *E. murphyi* to thrive, and gives likely opportunity for further expansion to new areas on Signy in coming decades. This species potentially has a major ecosystem influence by opening nutrient cycling bottlenecks, and its full (negative or positive) impact on the native ecosystem and communities remains to be evaluated. Thus, there is an urgent need

to investigate its role in wider ecosystem processes, as well as ensure appropriate biosecurity protocols are in place to minimise both the rate of population expansion on Signy Island and to prevent colonisation of other areas in the maritime Antarctic.

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AUTHOR CONTRIBUTIONS

The study was conceived by Bartlett, Convey and Hayward, and all data collection, field work and analysis was carried out by Bartlett. Pertierra conceived the MaxEnt analysis, which was executed by both Bartlett and Pertierra. All authors contributed to writing the paper.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting Information

Appendix S2: Supporting Information

Appendix S3: Supporting Information

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